THE FORGOTTEN ARTHROPODS: FOLIAR MITES IN THE FOREST CANOPY

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Walter, D.E., O'Dowd, D. and Barnes, V. 1994 06 30: The forgotten arthropods: foliar mites in the forest canopy. *Memoirs of the Queensland Museum* **36** (1): 221-226. Brisbane. ISSN 0079-8835.

Most studies of canopy invertebrates report few mites, yet mites were the most abundant arthropods in the upper canopies of rainforest trees and lianas around 3 forestry research towers in Queensland (means = 900 - 5,581 mites per m^2 of foliage). Within-site species diversity was high with 47 mite species being collected from just 46 leaves from the upper canopy (18-37m) in one tropical rainforest. Across-site diversity of leaf-inhabiting Parasitiformes (Phytoseiidae, Ascidae, Ologamasidae) was assessed using 2,818 slide-mounted specimens from eastern Australia. Of the 64 species identified, 30 were undescribed. A strong temperate to tropical increase in species richness was evident with little overlap (5%) in species between temperate and tropical forests. Foliar mites were a specialised fauna, generally absent from forest leaf litter. In temperate forests in Victoria, 28 species of oribatid mites were found on the leaves, stems, and trunk of musk daisy trees. Only 2 of the 18 species found on leaves and stems were also collected from soil-litter samples under the trees, indicating that the arboreal fauna is diverse, and distinct from that of the soil. ☐ *Acari, rainforest, canopy, biodiversity, Phytoseiidae, Ascidae, Oribatida.*

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Recent research in the canopies of tropical rainforests, relying primarily on chemical knockdown techniques, has discovered an amazing diversity of animal species, primarily insects. Mites, although they may be dominant in soils beneath the trees (Stork, 1991), appear to be uncommon in canopies, usually representing less than 7% of the total number of arthropods collected (Stork, 1988; Basset, 1991; Basset et al., 1992; Kitching et al., 1993). These studies leave the impression that mites are minor elements in the canopy fauna.

For the last three years, we have tried to develop an understanding of the interaction between foliar mites and leaf surface structures, especially leaf domatia (Walter, 1992; Walter & O'Dowd, 1992 a, b; Walter & Behan-Pelletier, 1993). Incidental to these studies, we have accumulated a large database on the abundance and diversity of foliar mites in Australian rainforests. Our results suggest that previous studies have grossly underestimated their abundance and diversity (Walter & O'Dowd, 1994). Rather than being relatively rare, arboreal mites are exceedingly abundant, by far the most abundant canopy arthropods. In the following paper, we support this statement with studies at three canopy towers in Queensland, Australia. We also present a preliminary analysis of species diversity at one tower, and discuss the diversity of predatory foliar mites across sites and regions in eastern Australia. Finally, we show that foliar mites are a small subset of the arboreal fauna, and that the mites in the forest canopy are diverse and distinct from those in soil under trees.

MATERIALS AND METHODS

Abundance & Diversity of Foliar Mites in Rainforest Canopies

Three research towers in Queensland: Pine Creek near Gordonvale (16°59'S, 145°50'E), Curtain Fig near Atherton (17°16'S, 145°34'E), and Mick's Tower in the Green Mountains area adjacent to Lamington National Park (28°13'S, 153°07'E) were used to reach upper canopies (to 37m) of rainforest trees and lianas. From decks at various levels of each tower, extendable pole-pruners were used to clip small shoots; 1-5 leaves were removed from each shoot, placed in plastic bags, and refrigerated until processing. Processing consisted of scanning each leaf under a stereomicrosope using cool light, dissecting any structures (domatia, galls, webbing, exuviae, detritus, etc.) with a scalpel, and counting mites on both leaf surfaces. Representatives of all distinguishable mite taxa were collected into 70% alcohol with a small brush; excess mites were crushed to avoid double counting. Eriophyoid

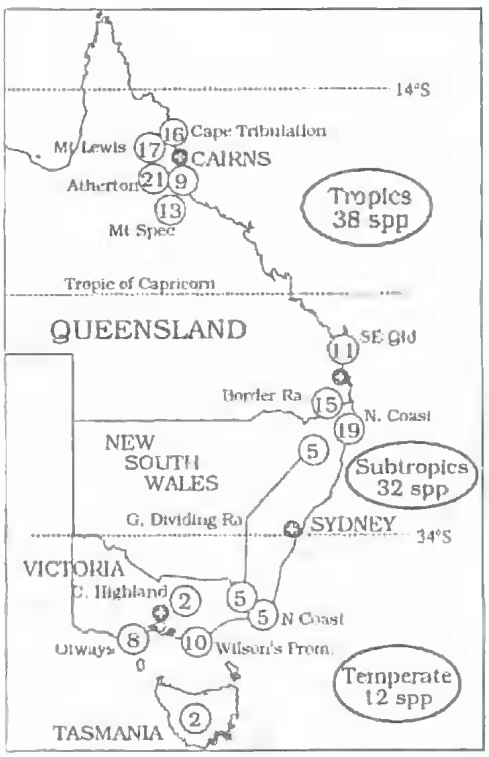

Fig. 1. Species diversity of foliar Parasitiformes. Predatory parasitiform mites (Phytosciidae, Ascidae, Ologamasidae) collected from the leaves of woody plants in Tropical, Subtropical, and Temperate Rainforests in eastern Australia showed a strong temperate to tropical gradient in species diversity. A total of 64 species was identified from 2,818 slide-mounted mites (see Table 3). Only two species occurred in both temperate and tropical rainforests (5%), but 22-23% of species were shared between adjacent climatic zones.

mites within galls were not counted (because they were too small, numerous, and difficult to extract), but any predatory or scavenging mites present in galls were collected. Mites were assigned to feeding guilds after Walter & O'Dowd (1994).

Site & Regional Diversity of Foliar Parasitiformes

Because of their importance in biological control, predatory parasitiform mites are relatively well known at the species level. We collected these mites from 13,266 leaves from 193 species of trees, shrubs, and lianas between 17 November 1990 and 1 May 1993. Except in Victoria, only rainforest vegetation was sampled, i.e. fire-protected or fire-resistant forests with closed-canopies composed of broad-leaved, evergreen vegetation not dominated by species of *Eucalyptus* or *Acacia* (Gell & Mercer, 1992). Tropical rainforest sites in North Queensland included Cape Tribulation (Daintree, Mossman), Cairns (Gordonvale to Mission Beach); Mt. Lewis, the Atherton tablelands, and Mt. Spec. Subtropical rainforest sites included SE Queensland (Fraser Island to Maroochydore), the North Coast of New South Wales (Kingsport to Myall Lakes); the Border Ranges (including Mt. Warning and the Nightcap Mts.), and the Great Dividing Range (Washpool National Park to Barrington Tops). Temperate rainforest sites included the South Coast (southcoast of N.S.W. and East Gippsland), Wilson's Promontory; the Great Dividing Range, Victorian Central Highlands, Otway Ranges, and Tasmania (Fig. 1). In Victoria, four sclerophyll forests and a mangrove site were also sampled. Leaf areas were measured on a image analyser (Image 3.0, Monash University, Clayton, Australia). Species identifications are based on mites cleared in Nesbitt's solution and mounted in Hoyer's medium on glass slides (Krantz, 1986).

Distribution of Oribatid Mites on Musky Daisy

Oribatida, mites that feed on fungi and scavenge detritus, and have strongly sclerotised adults that are easily sorted to morphospecies, were used to assess species distributions within a tree. Four strips of bark (each 16 cm^2), 6 segments of stem (each c. 15 cm long), and 8 leaves were randomly selected from each of 11 musk daisy trees (10 *Olearia argophylla*, one *O. lirata*) growing in warm to cold temperate rainforests in south-central Victoria. In addition, 4 cores of leaf litter (each 50 cm^2 and 2 cm deep) were randomly taken under the canopy of the trees about a half metre from the trunk. Samples were stored in plastic bags, refrigerated, and examined within 48 hours of collection. Bark, stem, and leaf samples were scanned under a stereomicroscope and mites collected as above. Soil samples were extracted using Tullgren funnels (60 watt light bulbs) over 70% ethanol for three days.

RESULTS

Abundance & Diversity of Foliar Mites in Rainforest Canopies

Upper canopy leaves were sampled from 5 trees species in lowland tropical rainforest near Pine Creek, 4 tree species in montane tropical rainforest at Curtain Fig, and 3 tree species and a furry

	Leaves	Predators	Herbivores	Scavengers	Total mites	foliage (m^2)	Mites / m^2
Curtain Fig Tower							
Aleurites moluccana	6	11	0	7	18	0.084	214
Argyrodendron peralatum	20	36	0	241	277	0.352	787
Diploglottis diphyllostegia	15	481	705	245	1431	1.082	1323
Toona australis	5	44	6	94	144	0.559	258
Total Examined	46	572	711	587	1870	2.077	
Pine Creek Tower							
Acacia aulacocarpa	45	2	0	6	8	0.069	117
Beilschmedia bancroftii	50	1	76	2	79	0.083	951
Flindersia pimentaliana	20	6	0	16	22	0.296	74
Polyalthia sp.	40	17	0	25	42	0.060	701
Sarcopteryx stipata	5	26	391	23	440	0.048	9203
Total Examined	160	52	467	72	591	0.556	
Mick's Tower							
Euodia micrococca	44	12	5	2	19	0.147	130
Parsonsia fulva	35	304	598	1859	2761	0.258	10684
Randia benthamiana	50	87	1	458	546	0.142	3856
Synoum glandulosum	35	217	6	1052	1275	0.301	4238
Total Examined	164	648	594	3485	4727	0.847	

Table 1. Foliar mite densities. Forestry research towers near Atherton (Curtain Fig), Gordonvale (Pine Creek), and Lamington National Park (Mick's Tower) were used to obtain leaves from the canopies of rainforest trees. Each leaf was examined under a stereomicroscope, mites were identified to family or generic level, counted, and assigned to a feeding guild (Walter & O'Dowd, 1993). Leaf areas were then measured with an image analysis scanner.

silkpod liana (*Parsonsia fulva* Blake) in montane subtropical rainforest at the Green Mountains. The leaves of every plant species sampled carried mites, and densities ranged from a low of 74 per m^2 on the leaves of a Queensland ash (*Flindersia pimentaliana* Muell.) at Pine Creek to a high of 10,684 per m^2 on leaves of the liana furry silkpod (Table 1). In total, 7,188 mites were collected from the 3.48 m^2 of foliage sampled with average densities of 1,063 mites per m^2 at Pine Creek, 900 per m^2 at Curtain Fig, and 5,581 per m^2 at the Green Mountains.

The species composition of the foliar mite fauna sampled at Curtain Fig Tower was investigated in detail. Five leaf samples taken at each of 4 heights (22-37 m) in the canopy of a red tulip oak (*Argyrodendron peralatum* [Bail.] Edlin ex Boas) contained 5 species of predatory mites and 14 species of scavengers. Similar samples taken at 3 heights (18-26 m) in an adjacent brown tamarind (*Diploglottis diphyllosetgia* [F. Muell.] Bail.) contained 2 species of herbivorous mites, 9 species of predators, and 13 species of scavengers. However, only 1 predatory and 3 scavenging species were shared between the 2 trees (10%). Single samples near the tops (36 and 26 m, respectively) of a candlenut (*Aleurites moluccana* [L.] Willd.) and a red cedar (*Toona australis* [F. Muell.] Harms) yielded an additional 8 species (2 herbivores, 4 predators, 2 scavengers), such that the total sample of 46 upper canopy leaves contained 47 species of mites. Additional understory samples of 15 red tulip oak leaves contained 6 mite species not collected from any of the upper canopy samples (Table 2).

Site and Regional Diversity of Foliar Parasitiformes. A total of 64 species of parasitiform mites were identified from the 2,818 slide-mounted mites examined (Table 3). All but one species (Ologamasidae) belonged to two closely related families, Phytoseiidae and Ascidae. A strong positive temperate to tropical species diversity gradient was apparent (Fig. 1), and there was little species overlap between the three rainforest climate types. Only two (*Typhlodromus dachanti* Collyer, *Typhlodromus novaezealandiae* Collyer) of the 38 species found in tropical rainforests were also present in temperate rainforests. Tropical and subtropical

	Height Above Ground (m)					
	37	30	26	22	5	4
Predators						
Lasioseius sp. c	+					
Bdellidae sp. 1	+					
Neocunaxoides sp. 1		+	+	+		
Amblyseius sp. d		+	+	+	+	+
Iphiseius sp. 1			+			
Rubroscirus sp. 1					+	+
Lasioseius sp. z						+
Zetzellia sp.						+
Scavenger / Microbivores						
Symbioribates sp.	+	+	+	+		
Scapheremaeus sp. L		+	+			
Scapheremaeus sp. G			+			
Oribatuloidea sp. 1			+			
Tydeidae sp. 2			+			
Scapheremaeus sp. 1	+			+		
Oribatuloidea sp. 2	+			+		
Tydeidae sp. o		+		+		
Tarsonemidae sp. s				+		
Tarsonemidae sp. y				+		
Tydeidae sp. f				+		
Scapheremaeus sp. s	+	+			+	+
Daidalotarsonemus sp.	+	+	+	+		+
Tarsonemidae sp. g		+	+	+	+	+
Tarsonemidae sp. w			+		+	+
Scapheremaeus sp. P			+	+	+	+
Eupodidae sp. 1			+	+	+	
Triophtydeinae sp.				+	+	
Malaconothridae sp. 1					+	+
Tydeidae sp. f2						+
Total Mite Species	7	8	13	t4	9	1t

Table 2. Within-tree distribution of mite species. At each of 4 levels (22-37 m) in a large red tulip oak (Argyrodendron peralatum) growing beside Curtain Fig Tower near Atherton in north Queensland, mite species were identified from 5 leaf samples. Additional samples were taken at 5 m (10 leaves) and 4 m (5 leaves) in two understory red tulip oaks. A total of 28 species of mites was found on 35 leaves sampled, with each level producing more species of predatory or scavenging mites. No herbivorous mites were discovered.

collections contained 56 species of which 13 (23%) were shared, and temperate and subtropical collections produced 36 species of which 8 (22%) occurred in both forest types.

Distribution of Oribatid Mites on Musky Daisy

A total of 2,116 oribatid mites were collected from on and under musk daisy trees in Victoria (Table 4). Twenty-eight species of oribatid mites were found on the leaves, stems, and trunks (6-17 species per site). All but one leaf-inhabitant was also collected from small stems, but none were found on the trunks of the trees, and only one foliar species (*Mycozetes* sp.) occurred in the leaf litter samples. Two species found on small stems (including *Mycozetes* sp.) and 5 additional species from the trunk were also present in litter samples. Leaf-litter and surface soil beneath the trees harboured over 40 species of oribatid mites.

DISCUSSION

Rainforest canopies are covered in mites, many species and uncountable numbers. This richness of animals must have consequences for the canopy system, especially those resulting from the feeding of the abundant predatory and scavenging mites. The prevalence of plant species with leaf domatia, and their predominant use by these feeding guilds, must have evolved over long periods of time (O'Dowd et al., 1991), and strongly supports the assumption of a functional relationship between arboreal mites and rainforest trees (O'Dowd & Willson, 1989; Walter & O'Dowd, 1992 a, b, 1994).

Our studies barely scratch the surface of the canopy mite assemblage, but they do show that previous studies have generally neglected or missed these animals. For example, Kitching et al. (1993) reported mites to comprise 1,503 of the 22,984 arthropods collected (6.5%) from subtropical rainforest canopies in the Green Mts. adjacent to Lamington National Park in Queensland. Kitching et al. (1993) used a chemical knockdown technique to sample many cubic metres of the canopy, and collected the resulting rain of arthropods on 90 m^2 of funnels (10 funnels of 0.5 m^2 x 2 samples x 9 sites). They found 17 mites per m^2 of funnel, the highest density of mites reported in any study from subtropical or tropical rainforests (Walter & O'Dowd, 1994). Yet our study, at the same site, indicated that the 3 trees and the liana that we sampled averaged 5,581 mites per m^2 of foliage. Clearly, chemical knockdown techniques provide only a minimum estimate of the true abundance and diversity of arthropods in rainforest canopies.

Our results assessing the oribatid mites associated with musk daisy show that arboreal species are rare in the soil beneath the trees, and

	Ascidae			Phytoseiidae								
	Arca	*Lasioseius*	*Arctoseius*	*Amblyseius*	*Euseius*	*Iphiseius*	*Okiria*	*Paraphytoseius*	*Phytoseius*	*Typhlodromus*	*Caliphis* Ologamasidae	Total Species	Mites Examined
Tropical Rainforest	6	6	0	12	1	1	1	2	3	6	0	38	896
Subtropical Rainforest	2	1	1	11	2	1	0	1	6	7	0	32	830
Temperate Rainforest	0	0	0	1	1	0	0	0	3	6	1	12	755
Sclerophyll Forest	1	0	0	1	1	0	0	0	3	6	0	12	337
Total Species	6	6	1	20	4	1	1	2	9	13	1	64	2818

Table 3. Species of Foliar Parasitiformes by Genus. Slide-mounted parasitiform mites (Ascidae, Phytoseiidae, Ologamasidae) collected from leaves of 193 species of trees and lianas from Tasmania to the Cape Tribulation Region in eastern Australia (see Fig. 1) were identified to species. Of 64 species identified, at least 30 (47%) are undescribed.

that the foliar fauna is a small subset of the total arboreal mite assemblage (6 of 28 species in this study). Surviving on a leaf surface, especially one like musk daisy leaves with a slick surface of appressed hairs and without domatia or other refugia, must be especially difficult for minute animals. Success on such a bleak habitat, exposed to alternate periods of bucketing rain and intense insolation, must require specialised physiological, morphological and behavioural adaptations not needed by mites in more cryptic habitats like soil and bark. However, a number of oribatid mite taxa are leaf specialists (Walter & Behan-Pelletier, 1993). This is also true for foliar Parasitiformes. Only 2 (*Arctoseius semiscissus* [Berlese], Ologamasidae sp. 1) of the 64 species we collected also occur in soil, and it seems likely that numerous other species inhabit the stems, trunk, epiphytes, and hanging humus that occur on tropical rainforest trees.

The case for biodiversity being centred in invertebrates in rainforest canopies is well established, but the portion mites represent in this cornucopia is unknown. Although foliar mite species are but a small fragment of the total canopy fauna, there do seem to be numerous species. Predatory mites showed little overlap within or between regions (Fig. 1), at Curtain Fig few predatory or scavenging mite species were shared between adjacent trees, and even within a tree, more species were discovered with each new level sampled (Table 2). How is the high diversity of generalised predators and scavengers maintained? No one knows, and we are unlikely to answer this question for mites or any other diverse group of animals if we continue to rely on solely on chemical knockdown techniques.

ACKNOWLEDGEMENTS

We thank Peter O'Reilly, O'Reilly's Rainforest Rest, for his kindness and help during our research, and the people at the Tropical Research Centre, CSIRO, Atherton for their help. Our research was often aided by courteous and knowledgeable rangers and foresters throughout eastern Australia, and we thank them and the Department of Parks, Wildlife and Heritage, Tasmania, the Department of Conservation and Environment, Victoria, the National Parks and Wildlife Service and the State Forests of New South Wales, the Queensland Forestry Commission, and the Queensland National Parks and Wildlife Service for their collection permits. This research was supported by the Australian Research Council.

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	Total Mites collected	Densities ($/m^2$)	Total Species
Leaves	436	1343	6
Stems	253	26	17
Trunk	31	440	14
Litter	1396	6350	40

	Percent Species Overlap		
	Leaves	Stems	Trunk
Stem	28	-	-
Trunk	0	15	-
Litter	2	4	10

Table 4. Arboreal Oribatid mite fauna. Oribatid mites were collected from leaves (88), small stems (9.9 m), and bark (704 cm^2) from main trunk of 11 musk daisy trees (*Olearia* spp.) growing in rainforests in Victoria. Mites were also extracted from cores of leaf litter and upper 2 cm of soil taken under each tree. The arboreal fauna was distinct from that in leaf litter. Of 28 species found on trees, only 7 (primarily from trunks) also occurred in leaf litter under trees.

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